5.—Discontinuous and Presumed Vicarious Plant Species in Southern Australia

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The details of distribution of discontinuous and presumed vicarious species pairs in south-western and south-eastern Australia are presented. Selected discontinuous species are listed and their distributions shown on outline maps, and these species are discussed in relation to the geological and climatic history of the Australian continent. It is suggested that some disjunctions may have their explanation in long-distance wind dispersal. Presumed vicarious species known to occur in the two regions are listed, and are discussed in relation to discontinuous species and geological and climatic history.

Introduction

Comparison of the vascular floras of south-western and south-eastern Australia has revealed the existence of several hundred species in common, of which some 35 have been selected for study according to the principles outlined in the section below entitled "Discontinuities between South-western and South-eastern Australia".

All are autochthonous species whose disjunction is well marked and which have no obvious mechanism whereby they may be dispersed over long distances by water or by animals. All but a few are restricted to the temperate area of southern Australia shown in Figure 1.

In addition, about 50 pairs of presumed vicarious species have so far been noted in the two regions.

The only previous comparison of the vascular plants of the two regions at the specific level appears to be that of Hooker (1860), who stated that 83 species were common to south-western and south-eastern Australia. He gave the number of such species for each genus but mentioned no specific names.

Discontinuous Species

The area occupied by a species is usually said to be discontinuous (or disjunct) if it is broken into two or more portions which are separated by a distance exceeding the "normal dispersal capacity" (Cain 1944) of propagules of the species. The determination of dispersal capacity must depend on experimental data, but an estimate of dispersal capacity may be obtained from the size and morphology of the propagules. Discontinuity may be assumed if the actual distance separating the populations exceeds this estimate.

Minor Discontinuities in Eastern Australia

In central and south-eastern Australia several examples of discontinuities are well known. *Eucalyptus cladocalyx* is of particular interest because of its discontinuous occurrences on Eyre Peninsula, Kangaroo Island and in the Flinders Range, even though the tree has been planted successfully in intervening areas, proving the suitability, at least for growth, of such habitats.

Other examples are *Acacia peuce*, occurring in several separated localities in central Australia and south-western Queensland, *Eucalyptus globulus* and *E. regnans*, both occurring in south-eastern Australia and Tasmania, *Dillwynia orecdoxa*, restricted to the Victorian Grampians and the Braidwood-Clyde Mountains area of New South Wales, *Schoenus turbinatus*, *Lasiopetalum ferrugineum* and *Phebalium dentatum*, all of which are discontinuous between the Sydney district and the Gibraltar Range in northern New South Wales, and *Eucalyptus nitens*, which is discontinuous between the northern and southern tablelands of New South Wales.

Specht *et al.* (1961) have described the disjunct distribution of *Eucalyptus elaeophora* (now to be known as *E. goniocalyx*, according to Johnson 1962) in South Australia, Victoria and New South Wales, while Willis (1962) mentions several examples of Tasmanian plants which are found only in the Grampians in mainland Australia (e.g. *Leptospermum nitidum* and *Pomaderris apetala*), a number of disjunctions between the Grampians and the area from East Gippsland to central coastal New South Wales (*Psilotum nudum, Davallia pyxidata, Howittia trilocularis, Dodonaea truncatiales*, and *Westringia glabra*) and one species which is unknown between the Grampians and north-eastern New South Wales (*Swainsona brachycarpa*).

The distances between the disjunct areas of the above species are mostly smaller than those of the species mentioned below, and some may well prove to be continuous when more information on dispersal capacity becomes available.

Discontinuities between South-western and South-eastern Australia

The examples listed below were obtained by a study of the published literature, combined with the examination of specimens from several Australian herbaria. No critical taxonomic work has yet been done, but in most cases specimens from the south-western and south-eastern populations of each species have been compared in their gross morphology.

On the basis of distance, these may be classed as major discontinuities. Most are separated by about 750 miles, and a few by a greater distance. It is not considered likely that

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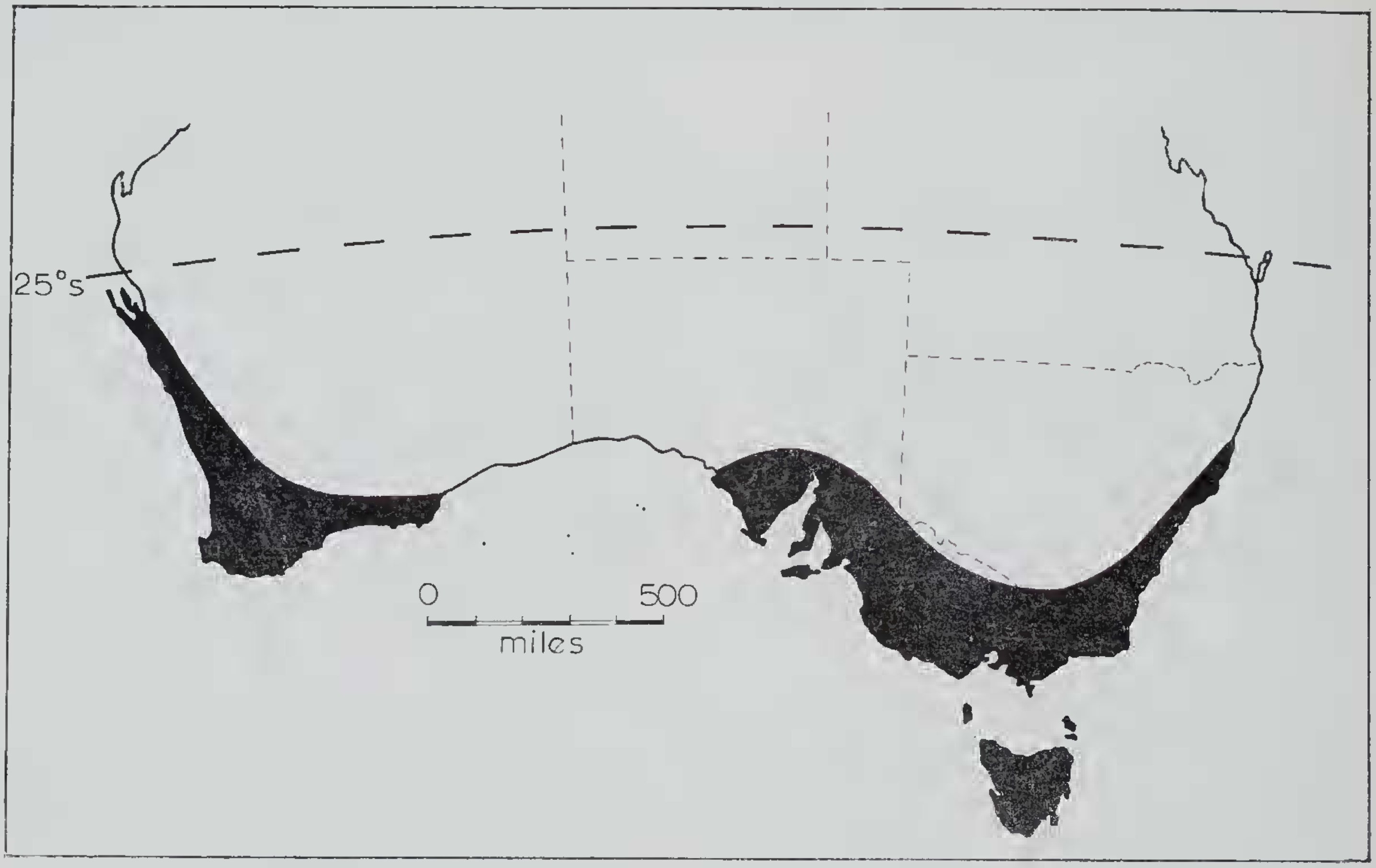

Fig. 1

additional collections would extend the ranges much further into the intervening area; the Nullarbor Plain is noted for its paucity of species, and the sclerophyll communities in which the majority of the species occur are certainly absent. In any case the existing habitat conditions suggest that their survival would be impossible.

It is considered that the distances involved here are probably greater than the normal dispersal capacity of propagules of these species.

In selecting a short list for study, the following classes of plants were eliminated from the several hundred apparently discontinuous species mentioned in the Introduction: (i) species capable of growing in semi-arid regions, because of their potential capacity of migration between the two regions by marginal spread; (ii) littoral species, because they are presumably capable of marginal spread along the coast, or dispersal by sea water or animals of the shore, without any great problem in establishment; and (iii) aquatic species of rivers and lakes, again without any apparent problems in dispersal or establishment. For the sake of simplicity, species having any occurrence outside temperate Australia and Tasmania have also been eliminated. The remainder, then, are those species whose disjunctions are most difficult to explain.

The speeies are listed below and their ranges are shown on the maps in Figures 2-3.

LILIACEAE
- *Borya nitida* Labill.
- *Calectasia cyanea* R.Br.
- *Lomandra micrantha* (Endl.) Ewart
- *Thysanotus tenellus* Endl.
- *T.* sp. (undescribed)

IRIDACEAE
- *Orthrosanthus multiflorus* Sweet

ORCHIDACEAE
- *Caladenia latifolia* R.Br.
- *C. menziesii* R.Br.
- *Corybas dilatatus* Rupp et Nicholls
- *Leptoceras fimbriatum* Lindl.
- *Microtis atrata* Lindl.
- *M. orbicularis* Rogers
- *Pterostylis robusta* (Ewart) Rogers
- *P. vittata* Lindl.
- *Thelymitra antennifera* Hook.f.
- *T. flexuosa* Endl.
- *T. fusco-lutea* R.Br.
- *T. macmillanii* F.Muell.
- *T. rubra* Fitzg.

PAPILIONACEAE
- *Daviesia brevifolia* Lindl.
- *Dillwynia cinerascens* R.Br.
- *D. uncinata* (Turcz.) J.M.Black
- *Sphaerolobium daviesiodes* Turcz.
- *S. vimineum* Sm.

RUTACEAE
- *Microcybe pauciflora* Turcz.

POLYGALACEAE
- *Comesperma polygaloides* F.Muell.

RHAMNACEAE
- *Cryptandra leucophracta* Schlecht.

STERCULIACEAE
- *Thomasia petalocalyx* F.Muell.

EPACRIDACEAE
- *Acrotriche cordata* (Labill.) R.Br.
- *Leucopogon hirsutus* Sond.

LOGANIACEAE
- *Logania vaginalis* (Labill.) F.Muell.

STYLIDIACEAE
- *Levenhookia pusilla* R.Br.
- *Stylidium perpusillum* Hook.f.

COMPOSITAE
- *Lagenophora huegelii* Benth.

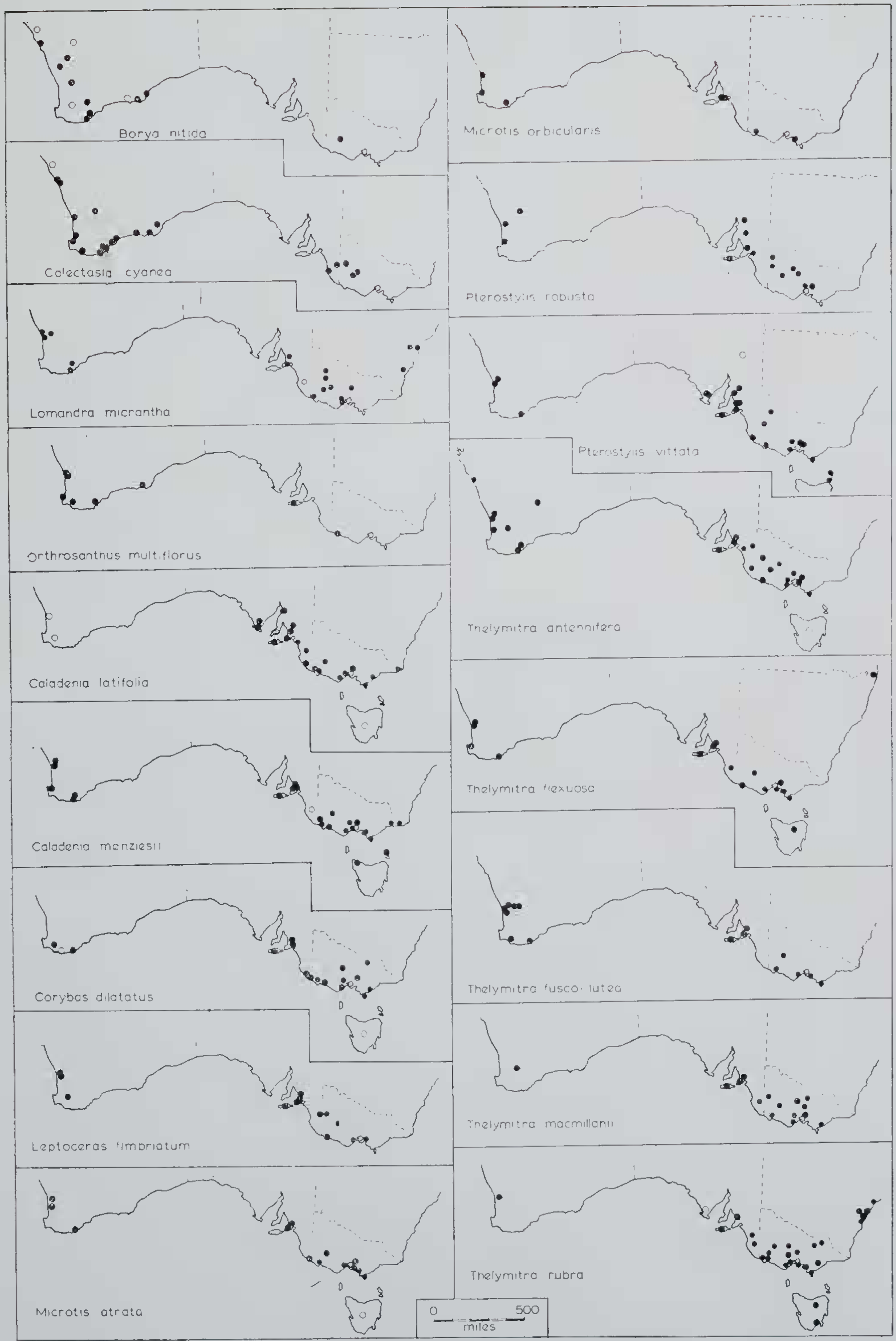
Borya nitida
Calectasia cyanea
Lomandra micrantha
Orthrosanthus multiflorus
Caladenia latifolia
Caladenia menziesii
Corybas dilatatus
Leptoceras fimbriatum
Microtis atrata
Microtis orbicularis
Pterostylis robusta
Pterostylis vittata
Thelymitra antennifera
Thelymitra flexuosa
Thelymitra fusco-lutea
Thelymitra macmillanii
Thelymitra rubra
0 500
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Fig. 2

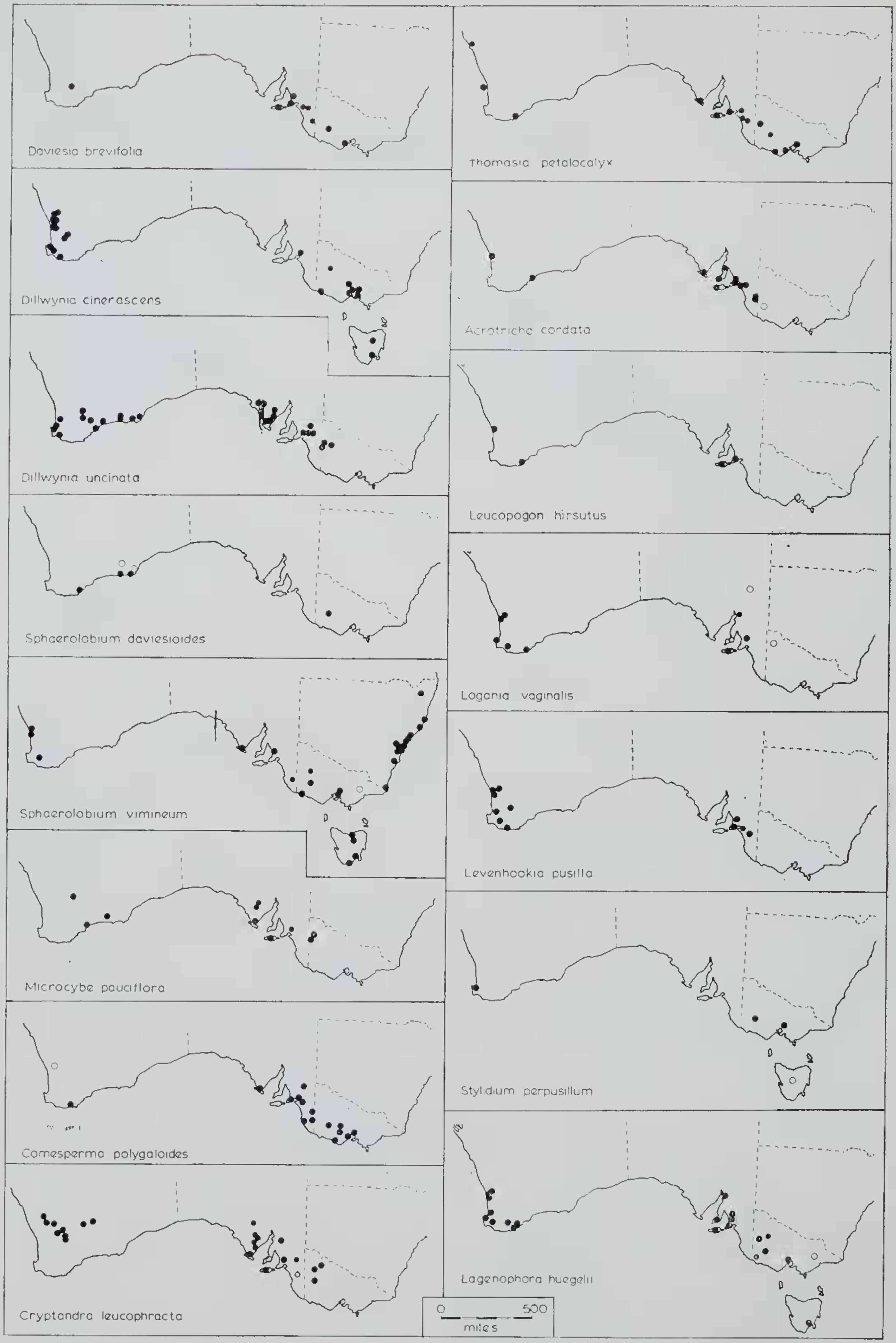
Daviesia brevifolia
Thomasia petalocalyx
Dillwynia cinerascens
Acrotriche cordata
Dillwynia uncinata
Leucopogon hirsutus
Sphaerolobium daviesioides
Logania vaginalis
Sphaerolobium vimineum
Levenhookia pusilla
Microcybe pauciflora
Stylidium perpusillum
Comesperma polygaloides
Lagenophora huegelii
Cryptandra leucophracta
0 500
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Fig. 3

There is no marked tendency for the majority of the species studied to be more widely distributed in either south-western or south-eastern Australia. *Borya nitida, Calectasia cyanea* and *Orthrosanthus multiflorus* are principally western with a limited occurrence in the east, while the reverse is true of *Sphaerolobium vimineum, Comesperma polygaloides*, and many of the orchids. *Leucopogon hirsutus* is very restricted in both regions. Three species, *Lomandra micrantha, Dillwynia cinerascens* and *Sphaerolobium daviesioides* have noticeably different forms in the two areas, the second being discussed in more detail below. *Thelymitara flexuosa* occurs in three separated areas, the eastern disjunction being over 750 miles. The widest disjunction is that of *Stylidium perpusillum*, which is not recorded between Busselton, Western Australia, and western Victoria, a distance of 1,560 miles.

It has been possible to pay special attention to the two species of *Dillwynia* which are discontinuous between the south-western and south-eastern regions. A large range of specimens has been examined from both regions showing that *D. uncinata* is markedly uniform in gross morphology over its entire area, while the disjunct populations of *D. cinerascens* seem to be morphologically distinct. All western specimens of the latter have spinescent branch-endings while all eastern specimens have none, and it appears that the two populations represent a pair of vicarious subspecies.

Presumed Vicarious Species

Closely allied to the concept of discontinuous species distributions is that of vicarious pairs or sets. The history of the latter has been summarized by Cain (1944) who defines vicarious species as "closely related allopatric species which have descended from a common ancestral population and attained at least spatial isolation." They are thus the equivalent of the *Artenkreise* of Rensch. As pointed out by Vierhapper (1919) (quoted by Löve 1954), it is possible to visualise two ways in which corresponding taxa in different areas may have arisen: (i) as *true vicariads*, which have penetrated into a new area and later become differentiated, and (ii) as *false vicariads* or *substitution taxa*, which have differentiated prior to their occupation of new areas. Löve is of the opinion that the terms *vicariism, vicariad* and *vicarious* should be confined to the second type, and suggests that where lack of information permits no such subdivision, only the collective term *corresponding taxa* should be used. This would apply to the Australian examples quoted below.

The concept of vicariism has been applied to taxonomic ranks other than species but, as mentioned by Turrill (1959), the phytogeographical significance of vicarious families, tribes or genera is often obscure. The concept has also been applied to communities.

The accompanying list (Table I) shows pairs of species in which the members of each pair appear to be closely related systematically and far removed geographically. In most cases Bentham's *Flora Australiensis* has been the primary source of information, and it has been verified that Bentham considered the species of each pair closely related. In some cases (marked with an asterisk) Bentham actually commented on the closeness of the relationship. Wherever appropriate more recent monographs and revisions have been consulted.

South-western species	South-eastern species
CYPERACEAE	
Lepidosperma angustatum R.Br.	*L. concavum* R.Br.
L. gracile R.Br.	*L. semiteres* F. Muell. ex Boeck.
L. leptophyllum Benth.	*L. tortuosum* F. Muell.
LILIACEAE	
Lomandra caespitosa (Benth.) Ewart	*L. sororia* (F. Muell. ex Benth.) Ewart
Xanthorrhoea preissii Endl.	*X. quadrangulata* F. Muell.
CASUARINACEAE	
**Casuarina decussata* Benth.	*C. torulosa*
C. trichodon Miq.	*C. stricta* Ait.
PROTEACEAE	
Adenanthos flavidiflora F. Muell.	*A. terminalis* R.Br.
Lambertia multiflora Lindl.	*L. formosa* Sm.
DROSERACEAE	
**Drosera rosulata* Lehm.	*D. whittakeri* Planch.
D. menziesii R.Br.	*D. planchonii* Hook.f.
MIMOSACEAE	
Acacia cochlicarpa Meissn.	*A. dallachiana* F. Muell.
A. divergens Benth.	*A. vomeriformis* A. Cunn.
**A. leptoneura* Benth.	*A. rigens* A. Cunn.
A. pentadenia Lindl.	*A. mitchellii* Benth.
PAPILIONACEAE	
Bossiaea spinosa (Turcz.) Domin	*B. foliosa* A. Cunn.
B. peduncularis Turcz.	*B. microphylla* Sm.
B. rufa R.Br.	*B. heterophylla* Vent.
B. biloba Benth.	*B. cinerea* R.Br.
Chorizema genistioides (Meissn.) C. A. Gardner	*C. parviflorum* Benth.
Daviesia anceps Turcz.	*D. alata* Sm.
Jacksonia sternbergiana Hueg.	*J. clarkii* F. Muell.
Mirbelia ovata Meissn.	*M. oxylobioides* F. Muell.
Oxylobium microphyllum Benth.	*O. cordifolium* Andr.
O. tricuspidatum Meissn.	*O. procumbens* F. Muell.
Pultenaea spinulosa (Turcz.) Benth.	*P. tenella* Benth.
RUTACEAE	
Boronia alata Sm.	*B. algida* F. Muell.
B. crenulata Sm.	*B. serrulata* Sm.
B. penicillata Benth.	*B. falcifolia* A. Cunn.
B. viminea Lindl.	*B. parviflora* Sm.
STACKHOUSIACEAE	
**Stackhousia pubescens* A. Rich.	*S. monogyna* Labill.
RHAMNACEAE	
Spyridium complicatum F. Muell.	*S. coactilifolium* Reiss.
STERCULIACEAE	
Lasiopetalum acutiflorum Turcz.	*L. ferrugineum* Sm.
DILLENIACEAE	
Hibbertia gracilipes Benth.	*H. billardieri* F. Muell.
H. crenata Andr.	*H. dentata* R.Br.
H. inclusa Benth.	*H. virgata* R.Br.
H. mucronata (Turcz.) Benth.	*H. acicualris* F. Muell.
THYMELAEACEAE	
Pimelea preissii Meissn.	*P. stricta* Meissn.
MYRTACEAE	
Darwinia sanguinea (Meissn.) Benth.	*D. micropetala* (F. Muell.) Benth.
Eucalyptus calophylla Lindl. }	{ *E. gummifera* (Gaertn.) Hochr.
E. ficifolia F. Muell. }	{ *E. intermedia* R. T. Baker
Leptospermum erubescens Schau.	*L. attenuatum* Sm.
Micromyrtus drummondii Benth.	*M. minutiflora* Benth.
EPACRIDACEAE	
**Leucopogon conostephioides* DC.	*L. rufus* Lindl.
**L. conostephioides* DC.	*L. deformis* R.Br.
L. gilbertii Stschegl.	*L. concurvus* F. Muell.
SOLANACEAE	
Anthocercis microphylla F. Muell.	*A. myosotidea* F. Muell.
GOODENIACEAE	
Dampiera altissima F. Muell. ex Benth.	*D. marifolia* Benth.

This is believed to be the first published list of presumed vicarious species pairs between south-western and south-eastern Australia. Wood and co-workers (Wood and Baas-Becking 1937, Wood 1949 and Wood and Williams 1960) have compared the species occurring in dry sclerophyll forests of South Australia, New South Wales and the Australian Capital Territory, but their examples of supposed vicarious species pairs appear to be little more than representative species of the various genera, chosen without regard to systematic affinity or even total geographic range. Three species of *Acacia* which are quoted are *A. myrtifolia* (representing South Australia, even though it also occurs in the other regions), *A. discolor* (New South Wales) and *A. falciformis* (A.C.T.). One of these is bipinnate and the two phyllodineous species are not closely related systematically.

Discussion

The present study has revealed the occurrence of geographically separated but systematically related populations in south-western and south-eastern Australia which show many different degrees of relationship. In some cases it has not been possible to differentiate the populations from the two areas, in others morphological differentiation has been at an infraspecific level, while further examples are given in which full specific distinctions are recognized, even though the populations are sufficiently similar to be considered true vicariads (i.e., presumably derived from an immediate common ancestor).

The existence of differentiated populations is most easily explained in terms of the Tertiary and Quaternary history of southern Australia, but in the case of discontinuous species in which the populations are morphologically indistinguishable it is felt that comparatively recent long-distance dispersal should be considered as a possibility.

It is likely that many of the species referred to above occupied former continuous areas which became broken up by the onset of unfavourable climatic conditions. Unfortunately, knowledge of the Australian flora of the upper Tertiary, Pleistocene and early Recent is scanty compared with that of the lower Tertiary. It is thought that the mid-Tertiary flora was a mesic one, that peneplanation was widespread and that the climate was humid and warm. Peneplanation was modified by vertical land movements beginning in the Miocene and culminating in the Upper Pliocene or Pleistocene, but the consequent climatic and edaphic changes are considered inadequate to explain the discrepancy between the distributions of Tertiary and present floras (Crocker 1959).

Crocker and Wood (1947) have suggested the existence of a Recent arid period, sudden and drastic enough to have had profound effects on a pan-Australian flora in the southern part of the continent. Their picture of the retreat of the pre-arid flora to refuge areas such as the Stirling Range, Mount Lofty Range, Grampians and Flinders Range is borne out by the present study of discontinuous species, many of which have been collected from two or more of these areas. Willis (1962) mentions several Grampians endemics "having undoubted Western Australian affinities." Crocker (1959) quotes the existence of "disjunct vicarious pairs, . . . major species disjunctions and the occurrence of relic species" as good evidence for the thesis of retraction and expansion.

Herbert (1929) quotes several species of *Eucalyptus* (e.g. *E. diversifolia* and *E. flocktoniae*) which are discontinuous between west and east, and suggests that their distribution is best explained by the onset of arid conditions in a previously well-watered central zone. He does not suggest a time for the climatic change.

Smith-White (1954) suggests that the areas of many species may have been simply bisected by the Miocene inundation of the Nullarbor Gulf, aided by a tract of arid country to the north, and that the bisection has been maintained to the present "in turn by physiographic, edaphic and climatic barriers".

Burbidge (1960) favours rather the late Pleistocene as the time of separation, on the basis of discontinuities between the two areas at the specific level.

The many degrees of morphological divergence between western and eastern populations may suggest that not all species were separated simultaneously. Stebbins (1950) points out that explanations in terms other than formerly continuous areas are possible, and mentions the possibilities of populations having always been separated although not to such a degree as at present and of the former existence of "stepping stones". The two extreme hypotheses (geological history and more recent long-distance dispersal) are not mutually exclusive, and combinations of the two are possible.

Overseas work on discontinuous species distributions has been summarised by Cain (1944). Most explanations have been based on past geological history, although often without direct fossil evidence. In some cases the discovery of fossil records from areas outside the living range of a species has given irrefutable evidence of contracting areas, but the necessary specific identification of the fossil specimens presents a formidable problem. In Australia we have no such records at the specific level which are likely to help elucidate west-east discontinuities. At the level of the subgenus, the occurrence of fossil leaves of corymbose eucalypts in Tasmania may point to the contraction of a former area occupied by a group of species, but gives no direct evidence at the specific level.

While geological history must be considered in explaining most discontinuities between south-western and south-eastern Australia, the possibility of propagules of certain species travelling long distances cannot be ruled out. Most objections to the general hypothesis of distance dispersal concern the establishment of propagules in a foreign environment, in competition with local species. Turrill (1959) has mentioned the ability of polyploids to extend into habitats unfavourable to their diploid progenitors but cautions against the drawing of broad conclusions. The role of vegetative reproduction as an aid to establishment is discussed by Baker (1953), and facultative apomixis could well be important. Taylor (1955) has discussed the establishment of alien species under natural conditions on Macquarie Island.

The instances of *Eucalyptus cladocalyx* and *E. ficifolia*, whose natural ranges are much smaller than in cultivation, may indicate a low capacity for dispersal or establishment, although these distributions may be of "young" species which have not had time to occupy all available habitats.

It will be noticed that a high proportion of orchids occurs in the list of discontinuous species set out above. Seeds of *Microtis atrata* were measured and found to be about 200 x 65 μ while those of *Thelymitra flexuosa* were about 180 x 100 μ. The smallest non-orcidaceous seeds were those of *Levenhookia pusilla* (about 500 x 220 μ). There seems no reason why seeds of this magnitude should not be carried long distances in the atmosphere. Ridley (1930) quotes examples of mineral particles 1/200th in. (1,270 μ) diameter being identified 970 and 600 miles from their respective sources and concludes by saying that "dust seed (Orchidaceae) . . . may travel a distance of as much as 700 miles" in one flight. Taylor (1955) suggests that species with very small seeds may have arrived on Macquarie Island as a result of wind transport, quoting as evidence the discovery of pollen grains of *Podocarpus* 600 miles from their nearest source of supply. Small (1921) quotes an experiment in which it was found that a light breeze of about two miles per hour is sufficient to support a dandelion fruit in the air indefinitely.

Accepting for the moment the possibility of wind dispersal having operated between south-western and south-eastern Australia, there is no climatological information to suggest the more likely direction. According to Kendrew (1937) and Gentilli (undated), southern Australia is characterised by prevailing winds in a general westerly direction in summer and easterly in winter, but there is much day to day variation. It is often assumed that the south-western region served as a centre of origin of many autochthonous species, on the basis of the high proportion and number of endemic genera found there.

There do not appear to be any well defined animal migration routes which could have carried propagules between the two areas in recent times. Aborigines are not likely to have carried seed deliberately for any distance although it is suggested that accidental carriage by aborigines may have occurred during their 8,000 year occupancy of Australia. Alternatively, early human occupants of this country may have disturbed the habitat sufficiently to create favourable conditions for the establishment of alien propagules carried by long distance wind dispersal.

With regard to the vicarious species, the main problems are the verification of true systematic affinity between the members of each pair, and the determination of whether the species are true or false vicariads. Löve (1954) has applied cytotaxonomic studies to corresponding types from North America and Europe and has shown 92 pairs of truly vicarious taxa and 41 pairs of substitution species, having different chromosome numbers. He has found that both vicarious and substitution types are to be found at different stages of separation, from habitat separation in the same region to physiographic or historic separation in different regions.

It is envisaged that future investigations will be undertaken in the following stages, with a view to obtaining further information relative to the foregoing observations:

(i) Field collection of material for detailed comparison of morphology, anatomy, cytology, breeding systems and habitat preferences (the information so far collected from herbarium labels has proved too scanty to provide useful comparisons of habitats).

(ii) Investigation of survival of small seeds in the laboratory under conditions of temperature and humidity likely to be encountered on a transcontinental journey.

(iii) Cultivation and crossing of western and eastern individuals, in order to obtain some measure of genetic divergence.

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